practically separated. The failure to recognize the tetrad structure of plant chromosomes until the late stages of the first meiotic division is evidently due to the close association and coiling of the paired chromatids.

According to Darlington (1929), homologous chromosomes at diakinesis and metaphase are held together only through the exchange of partners between pairs of chromatids. The chiasmas formed by exchange of chromatids evidently do hold the paired chromosomes together at the earlier stages, but at diakinesis and metaphase the homologous chromosomes are often associated where no chiasmas are present. In *Datura* there are no chiasmas at the late stages of the first meiotic division and the chromosomes are associated only at the ends (Belling 1927). In *Secale* many metaphase chromosomes are attached at one end with no apparent chiasma formation (Figures 4, 5 and 6). In many cases the chromosomes are in contact at their ends with no evidence of the existence of earlier chiasmas. Apparently the chromonemata can be attached at their ends without exchange of partners between pairs of chromatids. In *Lilium* the chromosomes at metaphase are apparently held together only by their chiasmas. The difficulty of separation of homologues seems to be dependent on the number of chiasmas present at metaphase. In *Secale* there is no evidence of unusual tension in the separation of homologues but in *Lilium* the paired chromosomes are pulled apart with some difficulty. Darlington finds that the short chromosomes with a single chiasma separate earlier than long chromosomes with several chiasmas.

Darlington's study of polyploid Tulips and Hyacinths does show that the degree of pairing of homologous chromosomes is dependent on the number of chiasmas formed at diplotene. Only two chromosomes can be associated at any one point at pachytene so that in triploids the homologous chromosomes always change partners. At diplotene only two chromatids are associated at any one point and the exchange of partners among chromatids forms the only connection between two or more homologous chromosomes. Darlington's explanation of the method of chromosome and chromatid association is of considerable value in interpreting the mechanism of crossing over and the chromosome behavior in polyploid species.

In triploids the bivalents are apparently separated with some difficulty at the first meiotic division while univalents appear to divide readily in most cases. Newton and Darlington (1929) suggest that the difference in the behavior of bivalents and univalents in triploids may be due to the differences in the constitution of the chromatids. In a bivalent the chromatids in each homologue may be from different parents, due to crossing over, while in a chromosome which has not been paired they are of the same origin. Occasionally a univalent appears to divide like a bivalent, but such a univalent may have been associated with the bivalents at an earlier stage so that it might consist of chromatids from different chromosomes.

According to Newton and Darlington (1929) the difficulty of separation of bivalent, and the ease of separation of univalent chromosomes must be due to a greater attraction between homologous chromatids than between sister chromatids. On purely *a priori* grounds there is no reason for supposing that such differences should exist. The fact that the chromatids are from different parents is no reason for supposing that they have a greater attraction for each other than chromatids from the same parent. In Orthopteran chromosomes, where the chromatids can be clearly observed, there is no indication that the association of sister chromatids is any different than the association of homologous chromatids. A stronger attraction between homologous chromatids than between sister chromatids would mean that only homologous chromatids would pair and as a result of such pairing no detectable crossing over could occur. Such an association is not in accord with genetic results in other genera.

The apparent difficulty of separation of bivalents compared with univalents is probably due to differences in the mechanical association of the chromatids. In *Lilium* the homologous chromonemata are coiled during metaphase and are connected by chiasmas. A single coiled chromonema would divide readily if the chromatids were associated according to Kuwada's interpretation, but the chromatids could not separate readily except in one plane. If these planes do not coincide in the bivalent then one pair of chromatids would separate only under considerable tension. There is evidence in *Lilium* that such differences between the two pairs of chromatids do exist (Figure 24). If there is any twisting of the homologues about each other, or if crossing over occurs, the difficulties in separation of coiled chromatids would be increased. In *Secale* the chromonemata are not coiled at the time of chromatid separation and the chiasmas are usually single and terminal. In these chromosomes there is no evidence that unusual tension is required to separate the chromosomes. The rare occurrence of univalents which behave like bivalents in the triploid Tulips and Hyacinths is probably due to some twisting of the chromatids about each other which would prevent easy separation.

PARASYNAPSIS AND TELOSYNAPSIS

In *Secale* and *Lilium* side by side pairing is essential to account for the relation of the homologues at diplotene and early diakinesis. The parasynaptic interpretation is the only one which is supported by cytological evidence in all genera which have been critically studied. The association of chromosomes in triploids described by Newton and Darlington (1929), and Belling's (1927) description of segmental interchange applied in more detail to the *Oenothera* problem of ring formation by Darlington (1929) has removed all remaining arguments for telosynapsis.

Recently telosynapsis has been described in *Secale* by Melburn (1929), but it is obvious from an examination of the figures presented that any conclusions drawn from such material are worthless.

PRE-REDUCTION OR POST-REDUCTION

The first meiotic division is generally considered to be the one at which the homologous chromosomes are usually separated (Wilson 1925, Robertson 1916), but there is good evidence that post-reduction also occurs (Wenrich 1916, Carothers 1926). When crossing over occurs there is little significance in these two terms because either meiotic division would be both reductional and equational for different segments of the same chromosome.

The invariable occurrence of pre-reduction must mean that sister chromatids are already bound together by the spindle fiber attachment at the leptotene or pachytene stage, or that the formation of nodes and internodes at diplotene is not a random process. The first suggestion is the more probable.

Where pre- and post-reduction occur in equal proportions in a particular chromosome (Wenrich, 1916) we must conclude that internode formation at diplotene depends on random association of chromatids and that the spindle fiber attachment does not unite associated chromatids until diplotene or later.

Invariable post-reduction will occur if homologous chromatids are bound together at the point of spindle fiber attachment at pachytene, or if internode formation is not a random process, but always occurs so that homologous chromatids are always associated at the point of fiber attachment. Post-reduction would also invariably occur if only homologous chromatids were paired, but in such a case crossing over could not be detected by genetic tests.

The fact that the chromosome segments are seldom, if ever, of the same genetic constitution at the point of the spindle fiber attachment in the "equational exceptions" described by Bridges and Anderson (1925) and by Redfield (1930) proves that in *Drosophila* the first meiotic division is invariably reductional. Both the cytological and the genetic evidence leads to the conclusion that regular post-reduction is exceptional.

THE MECHANISM OF CROSSING OVER

Janssens' earlier theory of crossing over has been discussed by Wilson and Morgan (1920) and his latest modification of the chiasmatype theory (Janssens 1924) has been considered in detail by McClung (1927). In his earlier discussion of crossing over Janssens assumed that the homologous chromosomes were twisted and broke at certain points of contact to reunite forming new associations which combined segments from each homologous chromosome. In his more recent paper he assumed that breaks might occur in the chromatids at any point where they were in contact. As the paired chromatids open out, the "chiasmas" represent points of segmental interchange between two homologous chromatids. Crossing over was described at various stages of meiosis including metaphase.

As Janssens' critics have pointed out, the chiasmatype theory of crossing over is not in accord with the cytological facts. The "chiasmas" are only optical phenomena and are formed by the alternate separation of different pairs of chromatids (Diagram 2). Since a detailed criticism of the chiasmatype theory of Janssens has already been presented by McClung it will be unnecessary to discuss it further at this time.

Belling (1929) has offered another explanation of crossing over, although it is presented only as a working hypothesis. He assumes that breaks occur in the chromatids at leptotene. When two breaks in different chromatids coincide at pachytene they may reunite to form a chiasma or point of segmental interchange between homologous chromatids. The chiasmas found at metaphase represent points at which crossing over occurs when the chromosomes divide.

As Newton and Darlington (1929) have pointed out Belling's theory of crossing over is based on the unproved assumption that the occurrence of one break will interfere with the occurrence of a second break in the adjacent sections of the chromatid. The theory can not be reconciled with the differences in chiasma formation in triploid and tetraploid Hyacinths (Darlington 1929). There is no explanation of the cause of numerous breaks in the chromatids, or if they do break, why they should reunite.

Morgan (1919) has suggested that the twisting of the chromosomes about each other in the early prophases might cause breaks in the chromatids so that sections of different chromatids would reunite. According to this theory crossing over is dependent on the twisting of chromonemata about each other at a number of points. This theory has little cytological support and does not meet all genetic requirements.

Several other theories have been presented to account for crossing over, but since they have such an inadequate cytological basis they need not be considered here.

In none of the theories presented is there an adequate explanation for the remarkable precision of crossing over so that duplication and deficiency of chromatid sections rarely occur. Nor is there any adequate reason why the chromatids should be recombined after they break.

No satisfactory interpretation of crossing over can be based entirely on the spermatocyte chromosomes of the Orthoptera, because in this group there is little cytological or genetic evidence that crossing over occurs in the males (McClung 1927, Nabours 1925). But if we assume, as seems probable, that chromosome behavior in plants and amimals is fundamentally the same, differing only in details, then our knowledge of Orthopteran chromosomes, combined with recent information concerning chromosome structure and behavior in plants, should serve as a basis for a logical interpretation of crossing over which is in accord with all genetic requirements.

The cytological interpretation of crossing over will be outlined, followed by the cytological evidence and a discussion of the genetic evidence.

THE CYTOLOGICAL INTERPRETATION OF CROSSING OVER

The homologous chromosomes become associated side by side at pachytene and are often more or less twisted about each other (Diagram 1). The chromonema of each chromosome is two-parted at leptotene although the sister chromatids may not be differentiated until pachytene or later. The pairs of chromatids may also be twisted about each other to some extent.

At diplotene the paired chromatids open out forming nodes and internodes. There is usually an alternate association of sister and homologous chromatids. The nodes represent points at which the chromatids change partners and are referred to as chiasmas. The maternal chromatids are pictured as black threads and the paternal chromatids as white threads (Diagram 2).

Between diplotene and metaphase the chromosomes contract about two-thirds of their length. In many species the paired chromatids do not contract during this period but form an apparently single spiral chromonema in each homologue. The relation of the chromatids during the earlier stages of chromosome contractions are shown in Diagram 3.

Due to the partial twisting of the chromosomes about each other at pachytene some of the internodes will be oriented so that two of the chromatids will come in contact where they cross each other at the chiasmas. Contact of chromatids at chiasmas will also occur due to the coiling of the chromonemata as shown in diagram 6. In this case the internodes open out at right angles to each other although only the sections of the chromonemata adjacent to the chiasma are represented. Beginning at the right end of this chromosome segment the coiling of both chromonemata is to the right, and at the chiasma the two crossed chromatids lie in one plane and are in contact with each other. Whether the chromatids come in contact due to twisting of the homologues or to coiling of the chromonemata, their subsequent behavior is the same. The paired chromatids on either side of the chiasma are closely associated and pairing of the chromatids, gene by gene, extends up to the point where the chromatids cross each other. The close association and coiling of the paired chromatids prevents any movement of the chiasmas and any strain imposed on the chiasma will cause the crossed chromatids to break at the point of contact. This strain on the chiasma could be induced by a further opening of the internodes, by unequal contraction of the two chromonemata, or by a slight amount of twisting of the chromonema as it coiled.

Breaks in the two chromatids occur at the same locus in most cases due to the close association of the paired chromatids. The free ends of the broken chromatids then pair, gene by gene, with the intact chromatids

until the broken segments of the different chromatids are brought in contact. In this way segments from different chromatids are combined.

Between early diplotene and metaphase the number of chiasmas is reduced, due to crossing over between different chromatids. In the chromosome represented by diagram 2, there are four chiasmas. Let us assume that crossing over occurs at chiasmas B and C. The relation of the chromatids at metaphase will then appear as shown in diagram 4. At this time, and probably at the earlier stages, the chromatids are so closely associated that they appear as a single coiled chromonema. In this diagram the association of maternal and paternal chromatids is indicated by cross lines.

The chiasmas which persist until metaphase are pulled apart as the chromosomes divide and at anaphase the four chromatids are completely separated except at the point of the spindle fiber attachment. The composition of the four chromatids resulting from this double crossover is shown in diagram 5. In the second division the chromatids, now the daughter chromosomes, are finally separated.

Crossing over between sister chromatids is not shown in the diagrams, but it could occur if there were preferential pairing between homologous chromatids, which is improbable. It could also occur if there were a twisting of the chromatids and pairing of homologous chromatids on either side of the twisted strands. Random association of chromatids, so that there is pairing between diagonal as well as adjacent chromatids, will result in crossing over between sister strands. With random associations of chromatids one-third of the crossovers should be between sister strands in diploids and one-fifth in triploids. Such a random association of chromatids is also improbable.

The present theory of crossing over is based on the fact that at diplotene there is an exchange of partners between paired chromatids at the chiasmas and that between diplotene and late diakinesis there is a reduction in the number of chiasmas. When extensive movement of the chiasmas is prevented by the close association or coiling of the paired chromatids, any reduction in the number of chiasmas must be due to breaks in the chromatids at the chiasmas so that segmental interchange occurs between two chromatids. This segmental interchange between two homologous chromatids is the cytological mechanism responsible for genetic crossing over.

THE CYTOLOGICAL EVIDENCE

The cytological evidence for this interpretation of crossing over is based on the work of McClung and his students with the Orthoptera, and on the recent work of Belling and Darlington, as well as the results of the present study of chromosome structure in *Secale* and *Lilium*.

In both plants and animals the homologous chromosomes pair side by side at the early prophase of the first meiotic division. The individual chromosomes may be longitudinally split before pairing as shown by

the work of Robertson (1916) and McClung (1928) and as indicated by the work on somatic chromosomes by Kaufmann (1926) and Sharp (1929). If the chromonema appears as a single thread at pachytene, which is often the case, the dual nature of the chromonema appears at later stages.

According to the cytological interpretation of crossing over two homologous chromatids must come in close contact with each other at chiasmas. This association of chromatids may be due to some twisting of the homologous chromatids about each other before or shortly after the diplotene stage, or to coiling of the chromonemata which would frequently cause the crossed chromatids to come in contact with each other at the chiasma. There is some evidence that a strepsinema stage occurs before or during early diplotene (Wenrich 1916, 1917, Robertson 1916, Janssens 1924). This twisting of the chromosomes occasionally persists to some extent to the later stages, but as a rule this torsion is undone as meiosis proceeds so that at metaphase the chromonemata on either side of a chiasma are in planes at right angles to each other. Strepsinema stages have also been described in many species of plants at both early and late prophase, but critical preparations show that twisting of synaptic chromosomes occurs only to a limited extent, if at all, at early and late diakinesis. Very little twisting of the chromosomes is necessary, however, to bring the crossed chromatids in contact at one or more chiasmas. Some such torsion seems necessary to produce apparently parallel chromosomes connected by a median chiasma as has been pictured at diakinesis in *Crepis* by Babcock and Clausen (1929).

There is no direct evidence that coiling of the chromonemata brings chromatids in contact at chiasmas, but there is adequate evidence that coiling of the chromonemata occurs in many plants and some animals. By means of wire models it can be demonstrated that such coiling will often bring the crossed chromatids into close contact at the chiasmas (Diagram 6).

In the Orthopteran chromosomes the associated chromatids change partners so that at diplotene different chromatids are paired in alternate internodes. The relation of the chromatids at diplotene is not so clear in plant chromosomes, but there is some evidence that the nodes are really chiasmas at this stage, and at metaphase when the chromosomes are pulled apart the chiasmas are frequently observed. It seems very probable that the relation of the chromatids at diplotene is the same in most plant and animal species.

There is no coiling of the chromonemata in the Orthopteran chromosomes at diplotene or later stages and the chromatids appear to be free to divide in a single plane. As the chromosome contracts and the diplotene loops open out, the chiasmas are free to move along the chromosome and are easily terminalized. In these chromosomes there is little chance for crossing over to occur.

In many plants and apparently in some animals the chromatids are closely associated and are coiled. In such chromosomes there can be no extensive movement or terminalization of the chiasmas before late metaphase. But there is a reduction of the number of chiasmas between diplotene and metaphase. In *Lilium* the total number of nodes or chiasmas is reduced from about thirty-nine at diplotene to about twenty-three at late diakinesis and metaphase (Belling 1928). A similar reduction of the number of chiasmas is also shown in *Tulipa* by Newton (1927). In *Secale* the average number of chiasmas in typical chromosomes is reduced from about four at diplotene to one or two at metaphase. The subterminal chiasmas in *Secale* are often terminalized but the median ones must break at the point of intersection of the crossed chromatids. If terminalization had occurred the dual nature of the chromonemata should be evident in the median sections of the chromosomes as it is occasionally at the ends.

The reduction in the number of chiasmas in these species must mean that in most cases the chiasmas which disappear between diplotene and diakinesis are due to breaks in the crossed chromatids. According to Belling (1928) "the nodes which disappear between diplophase and late diakinesis do not seem to be all or mainly twists. Nor do these vanishing nodes seem to be chiasmas which open out; for if so, this process should have been visible as it is at early anaphase." As has been shown in the diagrams such breaks would result in crossing over between two chromatids.

In some chromosomes as many as three or four crossovers are possible, although it is improbable that so many chiasmas would break at one division of a single chromosome. The average number of crossovers per chromosome appears to be about two in *Secale* and somewhat more than one in *Lilium* and *Tulipa*. Some of these crossovers may be between sister chromatids and could not be detected by genetic tests.

The cytological evidence for crossing over is not complete in all details and the actual breaks in the chromatids at chiasmas have not yet been observed. It seems very probable, however, that crossing over between homologous chromatids is associated with the reduction in the number of chiasmas between diplotene and diakinesis as Darlington (1929) has suggested.

THE GENETIC EVIDENCE

The genetic evidence for crossing over, especially in *Drosophila*, is now so complete that any theory regarding the mechanism involved can be thoroughly tested. The cytological interpretation presented in the preceding section seems to be in accord with the genetic results.

Time of Crossing Over

According to the genetic evidence crossing over must occur shortly after the pairing of homologous chromosomes. The cytological evidence

presented in the preceding section indicates that it occurs between diplotene and diakinesis. The effect of temperature on crossing over would seem to show that the segmental interchange between chromatids occurs at an early prophase stage (Plough, 1917). The potential amount of crossing over is determined to some extent by the number of chiasmas formed at early diplotene so that any treatment which would affect chiasma formation at this time might be correlated with the amount of crossing over, even though the actual breaks at the chiasmas do not occur until late diplotene or early diakinesis.

Crossing over occurs at the four-strand stage as was shown by Bridges (1916). Several cases of equational non-disjunction were found where one of the X chromosomes was a crossover and the other was not. Later this interpretation was more fully confirmed by an analysis of equational exceptions obtained from triploid females of *Drosophila* (Bridges and Anderson 1925). These results clearly indicate that crossing over occurs when the chromosomes are split into two strands or chromatids. This work also proves that crossing over occurs only between two chromatids at any one point. The present cytological interpretation is in accord with these genetic results, but the previous theories are not.

Gene Duplication and Deficiency

Crossover levels between the two chromatids seem to be remarkably uniform, but Sturtevant (1925) has found a case of unequal crossing over at the bar locus of the X chromosome in *Drosophila*. If the paired chromatids are not closely associated on either side of a chiasma it is possible for the crossed chromatids to come in contact so that a break will result in unequal crossing over. Such a relation of the chromatids and the results of unequal crossing over are shown in diagrams 7 and 8.

Sturtevant found that the order of the different genes was unchanged in duplicated and deficient sections of the chromosomes but the order of the two alellomorphs, bar and infrabar, may be BB′ or B′B. The order of alellomorphic genes will depend on the point at which unequal crossing over occurs.

Sturtevant's data indicate that the length of the chromosome is increased by duplication because the percentage of crossovers between forked and fused in normal bar stock is 2.5, but when the bar locus is double in each chromosome the percentage of crossing over between forked and fused is increased to 3.5. Apparently the unequal crossing over in this case involves an average length of one genetic unit.

Subsequent pairing between duplicated and deficient chromosomes will involve difficulties in the pairing of similar genes, although the elasticity of the chromonemata might permit pairing of similar genes in cases where only a very short section is involved.

The most remarkable fact concerning crossing over is the accuracy of chromatid exchange at the same level. The unequal crossing over at

the bar locus described by Sturtevant is exceptional, and is the only case recorded. Equal crossing over would be expected to occur if the associated chromatids are paired, gene by gene, up to the point of crossing of chromatids. This close association of the paired chromatids on either side of the chiasma would result in very short sections of the chromatids where crossing over is free to occur. In fact the pairing of similar genes in the associated chromatids would be expected to bring the point of crossing over to a region between the same two consecutive genes in each of the two chromatids involved in crossing over. The fact that the chromatid can contract about two-thirds of its length between diplotene and late metaphase suggests that at the time of crossing over, the gene elements may be separated by genetically inactive segments of the gene string.

Crossing over between Sister Chromatids

Crossing over between sister chromatids can only be detected by genetic tests in case of unequal crossing over, or perhaps by comparing the amount of crossing over in diploids and in triploids. Sturtevant (1928) has found no case of unequal crossing over at the bar locus of the X chromosome which is not accompanied by crossing over between forked and fused, so he concludes that in this region of the X chromosomes crossing over between sister chromatids does not occur. If pairing occurs between chromatids at random at the prophase of the meiotic division, then one-third of the crossovers in diploids and one-fifth of the crossovers in triploids will be between sister chromatids. A comparison of crossing over frequency in diploids and triploids should show whether or not crossovers occur between sister strands, but as Anderson and Bridges (1925) and Redfield (1930) have found, the differences between diploids and triploids show so much variation in different regions of the chromosome that any differential effect on crossing over, which might be caused by crossing over between sister chromatids, is completely masked.

There is no genetic evidence that crossing over occurs between sister chromatids, and the cytological evidence indicates that such crossing over must be exceptional. Crossing over between sister chromatids posits preferential pairing of homologous chromatids which is unlikely, and if such pairing is exclusive no genetic crossovers would occur. An occasional crossover between sister chromatids might be expected, due to the association of different homologous chromatids in two successive internodes, but such crossovers must be considered exceptional.

Interference

The phenomenon of interference was first observed by Sturtevant in 1913 and since that time it has been extensively studied by a number of investigators (Morgan, Bridges, and Sturtevant, 1925). In *Drosophila* chromosomes there is a modal interval between crossovers so that a break in one region interferes with a second break. Zero coincidence is found

for a certain distance, followed by an increase and then a second decrease, due to a second point of crossing over. The amount of coincidence is different for the three long chromosomes and varies in different sections of the same chromosome. The relation of the chiasmas and internodes seems to provide an adequate cytological explanation of interference. The genetic evidence indicates that the distance between crossovers is variable and Bellings (1928) description of *Lilium* chromosomes shows that the internode length is variable. The high coincidence in the middle of the third chromosome of *Drosophila* indicates that breaks in chiasmas are more likely to occur in two consecutive chiasmas where the internode length is comparatively long.

VARIATIONS IN CROSSING OVER

The amount of crossing over varies in different chromosomes and in different sections of the same chromosome (Morgan, Bridges, and Sturtevant, 1925). Crossing over would be expected to be a variable process if chiasmas are formed more or less at random and break only as the result of accidental twisting, unequal chromonema contraction, or other irregularities. Both the genetic and the cytological evidence is in accord with Morgan's (1925) conclusion that crossing over is an accidental by-product of the reduction division.

In *Drosophila* crossing over does not occur in the male and may be partially or completely inhibited in the female. There are several possible explanations to account for the lack of crossing over in the male. If only sister chromatids are associated at diplotene, there would be no chiasma formation and no opportunity for crossing over to occur. But due to absence of chiasma formation the association of homologues would be loose and considerable irregularity would be expected in the first meiotic division. There is adequate genetic and cytological evidence that such irregularity does not occur. Random pairing between only homologous chromatids would also prevent any detectable crossing over, but there is no reason to suppose that such pairing occurs, or if it occurs, why it should not occur in the female as well as the male. The only alternative seems to be that the association of the chromatids in the male is the same as in the female, but that in the male the chromatids can adjust themselves to changes in the chromosome during meiosis without breaking at the chiasmas as appears to be the case in the Orthoptera[1].

The Y chromosome of *Drosophila* is a special case because it shows no crossing over with the X even when it is present in the female (Bridges 1916). In secondary non-disjunction of an XXY female Bridges finds that pairing between XX occurs about four times as often as between XY. This difference in pairing of the X and Y chromosomes indicates that there is less attraction between the X and Y than between the X chromo-

[1]Huettner's description of the spermatocyte chromosomes of *Drosophila* which appears in a recent issue of the Zeit. f. Zellforschung indicates that there is a loose association of homologous chromosomes, but that a few chiasmas are formed and the first meiotic division is regular.

somes. Such a difference may be due to the absence of genetic factors, or it would occur if chromatid pairing in the Y is always between the sister chromatids. If only sister chromatids pair the X and Y could be associated only at the ends, which would result in loose pairing of the X and Y in normal males so that these chromosomes should divide before the division of the autosomes or tend to lag behind as univalents. Metz (1926) has found in several species of *Drosophila* that there is a loose association of the X and Y chromosomes at meiosis. According to Huettner (1930) the X and Y lag behind in the first spermatocyte division of *Drosophila melanogaster*, although apparently not as univalents.

Where crossing over is suppressed in all chromosomes of the female (Gowen and Gowen 1922), it is possible that pairing occurs only between sister chromatids. As has previously been pointed out, such pairing would result in a loose association of homologous chromosomes with the frequent occurrence of univalents at the first meiotic division and considerable irregularity in chromosome distribution. Gowen (1928) does find a relatively high proportion of chromosome duplication in the progeny of non-crossover flies.

This interpretation of the cause of no crossing over is supported by the work of Beadle (1930). He found that a single recessive factor caused asynapsis, or lack of chromosome pairing at meiosis, in *Zea*. The pollen of such plants is sterile, but some of the ovules are functional. When these asynaptic plants are pollinated with normal pollen about half of the progeny were triploids. Asynapsis leads to triploid production in *Zea* and is probably the cause of triploid flies in Gowen's non-crossover stock.

Asynapsis would occur if there is a differential rate of development between chromosome pairing and chromatid organization. If at leptotene the sister chromatids have already reached a stage of separation and development commonly found at diplotene then there can be no chiasma formation at later stages because the sister chromatids are already organized in pairs. The pairing between homologous chromosomes would be very loose, if it occurred at all. As a result no crossovers would occur, univalents would usually be found at diakinesis and metaphase, and irregular distribution of univalents would produce gametes with the haploid, intermediate, and diploid chromosome numbers. Asynaptic females crossed with normal males would produce aneuploid and triploid progeny. Apparently the pairing of sister chromatids in non-crossover stocks of *Drosophila* is not exclusive because rare crossovers are obtained (Gowen, 1929). In Beadle's asynaptic strain of *Zea* a few bivalents are often found.

A considerable number of crossover modifiers have been found in *Drosophila* which decrease or eliminate crossing over in certain chromosome segments (Morgan, Bridges, and Sturtevant, 1925). These variations in crossing over may also be due to preferential pairing of sister chroma-

tids in these regions. If preferential pairing of sister chromatids occurs over a considerable portion of the chromosome there should be a loose association of the homologues, and crossing over should be reduced or eliminated from a relatively long section of the chromosome. Bridges' (1916) work on high non-disjunction stocks of *Drosophila* seems to be of value in solving this problem. According to Bridges a high percentage of non-disjunction exceptions from XXY females means that the percentage of XY pairing is increased while pairing between XX is decreased. This change in the relations of the X and Y chromosomes would be expected if a genetic factor caused preferential pairing of sister chromatids for a considerable length of the X chromosome. The association between X chromosomes would be decreased because few chiasmas would be formed. The loose association between the two X chromosomes would result in an increase of XY pairing, which normally is very low. But such an association of sister chromatids would also decrease the amount of crossovers between the X chromosomes which do pair. It is perhaps significant that Bridges found crossover reducers in high non-disjunction stocks which decreased the amount of crossing over in the X chromosomes (Morgan, Sturtevant, and Bridges, 1925).

Crossing over would also be eliminated in chromosome segments if a chromosome with an inverted segment paired with a normal chromosome as Sturtevant (1926) has found. The cytological explanation is obvious.

Crossing over in Triploids

If the present cytological interpretation of crossing over is correct it must also be in accord with the crossover relations found in triploids. In triploid females of Drosophila crossing over has been found to occur between all three of the X chromosomes (Bridges and Anderson 1925) and between the three third chromosomes (Redfield 1930). In both cases two types of double crossovers were found; recurrent crossovers where the second crossover involves the same two chromosomes as the first, and a progressive type in which the second crossover takes place between different chromosomes from the first. These two types of crossovers occur with equal frequency. Appropriate genetic tests have permitted an analysis of the two chromosomes which pass to the same egg cell.

The behavior of the chromosomes in triploid Hyacinths described by Darlington (1929) seems to offer an explanation of triploid crossing over. When three homologous chromosomes pair at pachytene only two of them are associated at any one point so that an alternation of partners occurs. The association of three such homologous chromosomes at pachytene is represented by diagram 9. At diplotene chiasmas are formed between any two of the three chromosomes as shown in diagram 10. At the first reduction division two of the three chromosomes pass to one pole. The equational division separates paired chromatids.

In the hypothetical trivalent, shown in diagram 10, let us assume that crossovers occur at chiasmas 1, 3, and 5. The spindle fiber attachment is at the left end. We will assume that chromosomes A and B pass to the same pole at the first meiotic division. The chromatid constitution for the different segments of these two chromosomes will be $\frac{AAAA}{ABBB}$ and $\frac{BAAC}{BBCA}$. The second reduction division will then separate paired chromatids so that the two chromatids received by the egg cell will be $\frac{AAAA}{BAAC}$, or $\frac{AAAA}{BBCA}$ or $\frac{ABBB}{BAAC}$ or $\frac{ABBB}{BBCA}$. Three of these associations of chromatids would result in "equational exceptions" since for part of their length the two chromatids are alike. Crossing over between three chromosomes may be progressive or recurrent. In the above case only progressive crossovers occur, but if chromosome C paired with A instead of B, which would be equally probable, then recurrent crossovers would be obtained. With random association of the three homologous chromosomes, recurrent and progressive crossovers should occur in equal numbers.

In both the X and the third chromosome of *Drosophila*, regions in which the genes are closely spaced on the diploid map are lengthened on the triploid map, and regions in which the genes are far apart in the diploid are shortened in the triploid. The work of Muller and Painter (1929) and of Dobzhansky (1930) seems to throw some light on the possible cause of these differences in crossing over. These investigators found, that in the third chromosome the regions where the genes are closely spaced on the genetical map are far apart on the cytological map and *vice versa*. Such a relationship suggests that in regions where the genes are closely spaced on the genetical map, the average internode length between chiasmas is relatively long. The occurrence of long internodes would indicate that there is preferential pairing of chromatids in such regions. Such preferential pairing is probably caused by the physical relations of the chromosomes at the time of pairing rather than any preferential attraction between different chromatids.

When three chromosomes pair there may be preferential pairing of two chromosomes in the region where long internodes occur in diploids or the chromosomes may change partners in this region. In either case the number of chiasmas will be increased in this region in the triploid. In the trivalent shown in diagram 10, let us assume that in the diploid the internode length frequently extends from chiasma 1 to chiasma 4. In the triploid two additional chiasmas are formed in this region. Thus crossing over in triploids would be increased in regions where genes are closely spaced in the diploid.

In regions where the internode lengths are short in the diploid the intercalation of the third chromosome between two chiasmas would not

be expected to occur, so that for regions where the genes are widely spaced on the diploid map crossing over in the triploid would be reduced one-third.

SUMMARY

In *Secale cereale* each of the homologous chromosomes at metaphase of the first meiotic division contains a single coiled chromonema. The direction of coiling of the chromonema, in respect to the point of spindle fiber attachment, seems to be the same for any two homologous chromosomes.

During metaphase the chromonemata contract and become uncoiled. The chromonemata do not divide into separate chromatids until the chromonemata are uncoiled, although doubtless the two chromatids retain their identity from early prophase.

Between diplotene and metaphase the chromosomes shorten about one-third, but the chromonemata retain their original length by coiling. During metaphase the length of the chromonema is reduced about one-third while the length of the chromosome remains essentially the same.

In *Lilium regale* coiled chromonemata are also found at metaphase. The first meiotic division begins while the chromonemata are coiled. As the chromosomes are pulled apart the spindle fiber ends of the chromonemata are straightened out. The chromosomes are apparently separated with difficulty. When the division is nearly completed the chromonemata are pulled out into more or less straight rods. At this time the two chromatids of each chromonema can be identified. When the division is complete the chromatids contract and become more or less coiled. At early telophase each daughter chromosome appears as two coiled chromatids held together only at the point of the spindle fiber attachment. During metaphase and anaphase there is some shortening of the chromonemata but it is always longer than the chromosome when free from tension.

The coiling of the chromonemata, in *Secale* at least, is not a mechanism essential for the preservation of the linear order of the genes.

A comparison of *Secale* and Orthopteran chromosomes indicates that coiling of the chromonema is due to a differential rate of contraction between the chromosome and the chromonema.

The relations of the chromatids during the meiotic divisions are fundamentally the same in both plant and animal chromosomes. The nodes, or chiasmas, represent points where the chromatids exchange partners.

In plants the individual chromatids are closely associated in an apparently single chromonema and the tetrad nature of the bivalent chromosome is not clearly evident until late metaphase or anaphase.

Between early diplotene and late diakinesis the number of chiasmas is reduced, due primarily to breaks in the chiasmas. Such breaks would result in crossing over between the two chromatids involved.

A cytological interpretation of crossing over has been presented, based on the reduction in numbers of chiasmas between diplotene and late

diakinesis. This interpretation of crossing over seems to be in accord with all of the genetic requirements.

The genetic phenomena of interference, gene duplication and deficiency, variations in crossing over, and crossing over in triploids, have been discussed in their relation to the cytological mechanism of crossing over.

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DESCRIPTION OF PLATE 25

All figures were drawn from smear preparations of pollen mother cells. Figures 1 to 19 inclusive are magnified 2700 times; figures 20 to 26 inclusive are magnified 1600 times.

SECALE CEREALE

Fig. 1. A typical chromosome at diplotene showing nodes and internodes.
Fig. 2. Three chromosomes at early diakinesis showing the number and distribution of nodes and internodes.
Fig. 3. A typical association of homologues at late diakinesis.
Figs. 4–6, Metaphase chromosome with coiled chromonemata.
Fig. 7. All seven chromosomes at metaphase showing the different types of chromosome pairing.
Fig. 8. A vertical ring chromosome with a chiasma at one end.
Figs. 9–12. Chromosomes at late metaphase showing less coiling of the chromonemata and the dual nature of the chromonemata.
Fig. 13–15. Chromosomes at late metaphase showing the straightening of the chromonemata and the separation of the chromatids.
Fig. 16. Two chromatids at late anaphase.
Fig. 17. A daughter chromosome at telophase.
Fig. 18. A chromosome at interphase. The two chromatids are held together only by the spindle fiber attachment.
Fig. 19. The seven chromosomes at the second meiotic division.

LILIUM REGALE

Fig. 20. A chromosome with nodes and internodes at diplotene.
Figs. 20–22. Metaphase chromosome with coiled chromonema. Alternate internodes at right angles to each other.
Fig. 21. Early anaphase as the chromosome begins to divide. No separation of chromatids.
Fig. 22. Later stage of first meiotic division showing dual nature of chromonemata and the relations of the chromatids at the chiasma.
Fig. 23. Unequal separation of chromatids.
Fig. 24. Late anaphase with one pair of chromatids in contact while the other pair have separated and contracted.
Fig. 25. A typical daughter chromosome at early telophase showing contraction and coiling of the chromonema.

DESCRIPTION OF PLATE 26

Diagrams illustrating the cytological mechanism of crossing over.
Diagram 1. Pairing of chromosomes at pachytene. The chromosomes are slightly twisted about each other and are separated into their respective chromatids. The maternal chromatids are pictured in black, the paternal chromatids in white.

Diagram 2. Diplotene looping and the formation of nodes and internodes. The exchange of partners between paired chromatids constitutes a chiasma.

Diagram 3. Later diplotene stage as the chromatids become closely paired and form a coiled chromonema. Due to a partial twisting of the chromonemata, about each other or to the coiling of the chromonemata, the chromatids which appear to cross each other at the chiasmas will often be brought in contact with each other.

Diagram 4. Early metaphase. Chiasmas B and C have broken between early diplotene and late diakinesis. Since the close association and coiling of chromatids prevents appreciable movement of chiasmas any stress imposed on the chiasmas, due to unequal contraction of chromonemata, to opening of diplotene loops, or torsion caused by chromonema coiling, will cause breaks in some of the chiasmas. The association of two independent chromatids, one from each parent, into an apparently single chromonema, is indicated by cross lines.

Diagram 5. The four chromatids at late anaphase showing the results of the double crossover. The associated chromatids separate at the second meiotic division.

Diagram 6. Due to coiling of the chromonemata two chromatids may be brought in contact with each other even though the adjacent internodes lie in planes at right angles to each other as shown in this diagram. Gene by gene association in the paired chromatids will cause pairing of the associated chromatids up to the point of exchange of partners, so that breaks in the chromatids are confined to a very small segment of the crossed chromatids, and will result in precise crossover levels between the two chromatids.

Diagrams 7–8. These diagrams show the relations of the chromatids which would result in unequal crossing over. The order of the two alellomorphic genes B and B′ in the duplicated section will depend on the point where crossing over occurs.

Diagrams 9–10. The relations of the three homologous chromosomes at pachytene and at diplotene in triploids. These relations of the chromosomes and chromatids are based on Darlington's description of the chromosomes in triploid Hyacinths and seems to be in accord with genetic results obtained from *Drosophila* triploids.

CHROMOSOME NUMBERS IN QUERCUS

HALLY JOLIVETTE SAX

THE genus *Quercus* is divided into three subgenera, *Cyclobalanopsis* *Erythrobalanus* and *Lepidobalanus*. These subgenera include more than three hundred species of Oaks. They are found in the temperate regions of the northern hemisphere and in the tropics at high altitudes. They range south to Colombia in America and to the Malay Archipelago in Asia.

There are many hybrids known among the Oaks. Trelease says "So far as my knowledge goes, no hybrids have been detected except between parents of a single subgenus though supposed crosses of the aberrant red oak, *Q. Emoryi*, with the white oaks, *Q. grisea* and *Q. pungens* are reported." Crossing is usually found between very closely related species within the subgenus. Trelease reports fifty-one hybrids in the United States.

The Arnold Arboretum includes among its collections many pure

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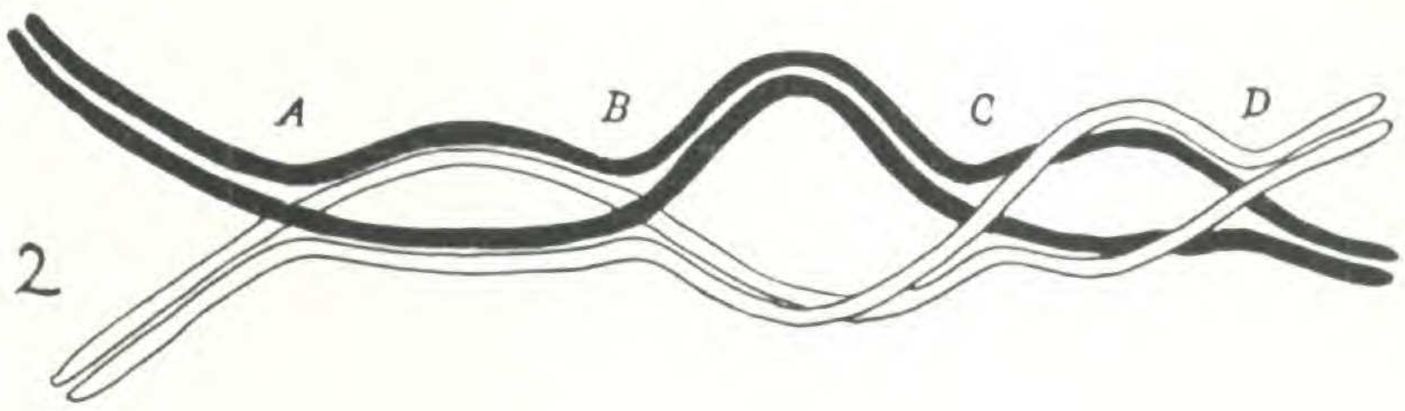

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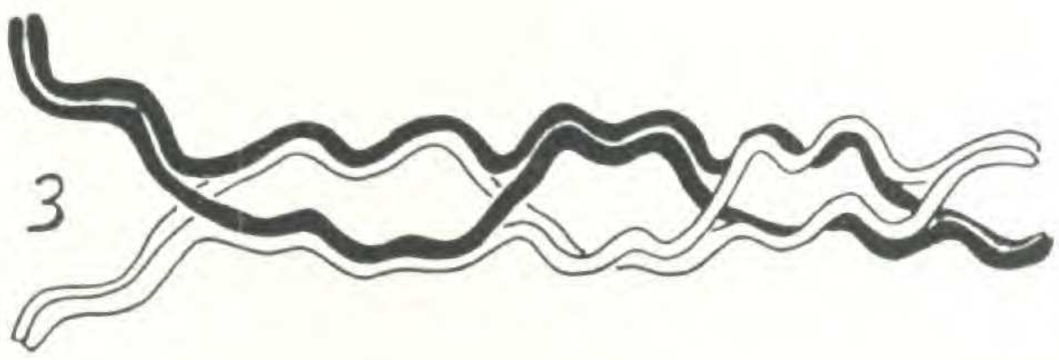

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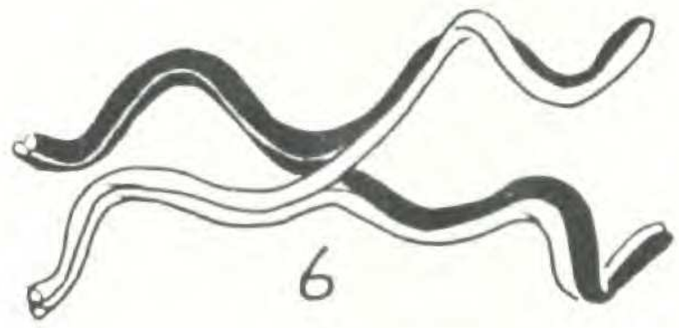

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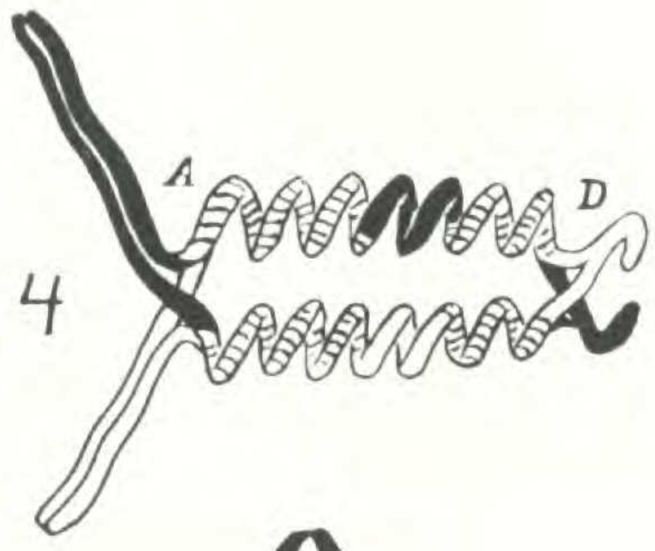

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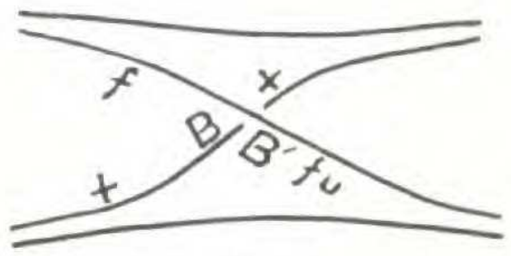

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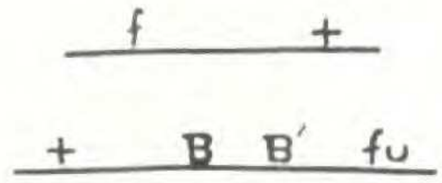

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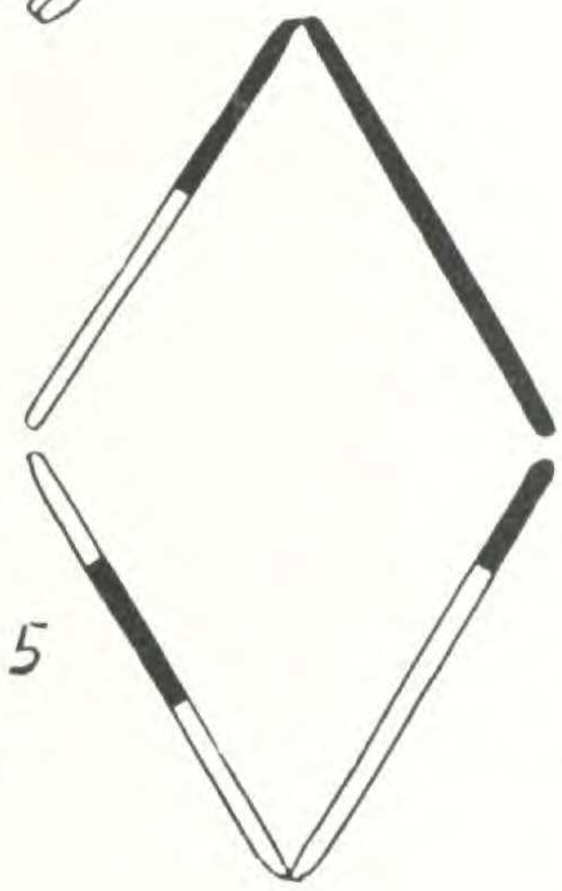

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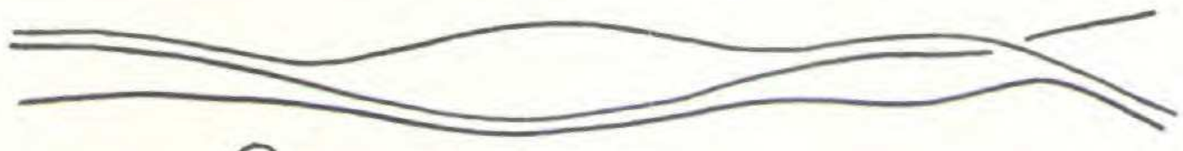

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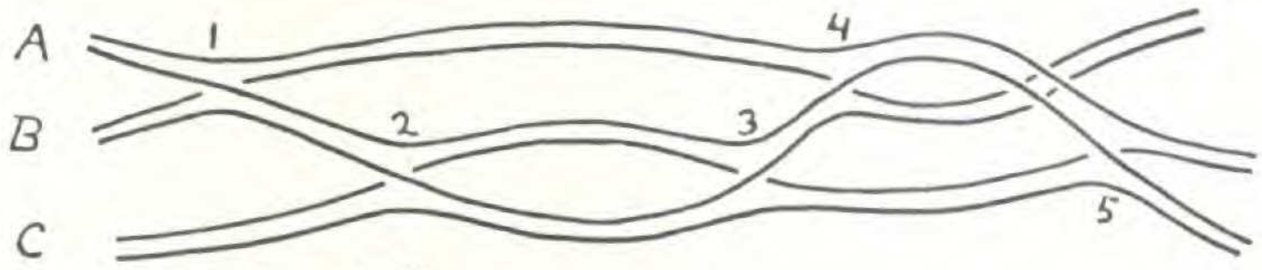

10

THE MECHANISM OF CROSSING OVER

species and hybrids of *Quercus*. A number of these were studied to determine the number of chromosomes, the size of pollen grains, and the amount of pollen grain sterility.

The first report on chromosome number in *Quercus* was given by Cosens in 1912. He reported eight chromosomes as the somatic number in *Q. coccinea* Muench.

Wetzel, in 1928, reports eleven as the reduced number for the following species: *Q. coccinea* Wangh., *Q. Dalechampii* Tenore, *Q. glandulifera* Blume, *Q. Koehnei* Ambrozy (*Q. Ilex* × *sessiliflora ?*), *Q. libani* Oliv., *Q. macranthera* Fisch. & Mey., *Q. pontica* K. Koch, *Q. robur* L., *Q. sessiliflora* Salisb. (*Q. sessilis* Ehrh.). The chromosome numbers in the above species were obtained by studying the divisions in the pollen mother cell. The number of somatic chromosomes, determined by studying nuclear divisions in the root-tips, was found to be twenty-two in *Quercus Cerris* L. and *Quercus nigra* L.

In 1929 Grimpu reported the number of chromosomes found in the following species: *Q. suber*, *Q. Ilex*, *Q. coccifera*, *Q. palustris*. He found twelve to be the reduced number. He studied the somatic chromosomes in *Q. cerris* and found twenty-four chromosomes.

Friesner, in 1930, published the chromosome number in ten species of Quercus: *Q. alba*, *Q. macrocarpa*, *Q. Prinus*, *Q. Michauxii*, *Q. Muhlenbergii*, *Q. borealis* var. *maxima*, *Q. velutina*, *Q. coccinea*, *Q. marilandica*, and *Q. prinoides*. He reports twelve as the diploid number of chromosomes in the roots of each of the ten species.

The species of *Quercus* studied in the present work belong to the subgenera *Erythrobalanus* (the Red and Black Oaks) and *Lepidobalanus* (the White Oaks). All the hybrids are from crosses between species of the same subgenus.

The chromosome number was determined from the divisions in the pollen mother cells. Very good figures were obtained from acetocarmine smears. Although the chromosomes were very small, it was possible to get clear figures by this method.

The counts are given in the table included below which gives the species, the place of origin, the number of chromosomes, the average size of the pollen grains and the percentage of sterility found in each species.

In most species the number of chromosomes was very distinctly twelve. In some cases, there were apparent only eleven chromosomes; in others thirteen chromosomes could be counted. As reported by Grimpu, there seems to be some irregularity in the meiotic division due to the loose association of the chromosomes. In all cases the number was 12 or 12 ± 1. The hybrids show the same number. From the table there appears to be a remarkable uniformity in number when the species are of the same or of different subgenera or when they are pure species or hybrids.

Since pollen grain size is usually considered an index to relationship of chromosome number within a genus, measurements of the pollen

grains in the above and additional species were made. Mature pollen grains were mounted in aceto-carmine. They were then measured by means of an ocular micrometer. In order to avoid differences due to swelling on applying aceto-carmine, the spores were measured at the same intervals of time in the different species after fixing. A large number of pollen grains were measured. From these the average size of the grain was computed. The data are given in Table I.

The size of the pollen grains in the different species ranges from 6.8 to 8.7 units with the exception of *Q. dentata*. In this species pollen was taken from two trees, one having pollen grains of 8.7 units in diameter, the other 11.2. It is noteworthy that there is the same range of variation in size of pollen grains in the species where the chromosomes have been counted and have been found to be 12 or 12 ± 1 as there is where no counts were made, excepting the one unusual case of *Q. dentata*. It would be interesting to determine the chromosome number in both specimens of *Q. dentata* to see if there is any cytological variation connected with the morphological differences.

The amount of pollen grain sterility in the different species was determined by counting the number of poorly developed pollen grains in a field as well as the total number. Several counts were made and the percentages of sterility calculated for each species.

Table I includes the data on sterility. The sterility ranges from three to ten percent with the exception of one of the two trees of *Q. dentata*. This tree, which also had the exceptionally large pollen grains, showed eighty percent sterility. The other specimen of *Q. dentata* had eight percent pollen sterility. This does differ significantly from that of other species. With one exception, there is really no significant difference in sterility between the different species and the hybrids studied. There is a striking uniformity in fertility both in pure species and in hybrids. *Q. ludoviciana*, *Q. Leana*, *Q. exacta*, *Q. Bebbiana*, and *Q. Sargentii*, all hybrids, show no significant difference in sterility from that found in pure species.

The uniformity in chromosome number, in the pollen grain size and pollen grain fertility among both pure species and the hybrids is remarkable. There is a large number of natural hybrids with apparently fertile pollen within the subgenus. Thus in the Oaks we find great variability in morphological characters and a wide geographical distribution with uniformity in chromosome number.

Much of the variability in the morphological characters of *Quercus* is doubtless due to hybridization but it is not associated with any irregularity in chromosome distribution.

DATA ON QUERCUS

Quercus	Chromosome number	Pollen size	Pollen St. %	Habitat
Erythrobalanus				
Q. ludoviciana ×	12 ± 1			N. America
Q. imbricaria	12	7.5	4	N. America
Q. Leana ×	12 ± 1	7.4	8	N. America
Q. exacta ×	12	7.4	7	N. America
Q. ilicifolia		7.9	6	N. America
Q. velutina	12 ± 1	7.0	7	N. America
Q. coccinea		7.7	4	N. America
Q. palustris	12	6.9	6	N. America
Lepidobalanus				
Q. serrata		7.3	6	Asia
Q. Cerris		8.0	3	Asia
Q. macranthera		7.9	6	Eurasia
Q. robur		6.8	10	Europe, N. Africa, West Asia
Q. haas		7.8	7	Asia Minor
Q. alba	12	7.5	3	N. America
Q. Bebbiana ×		7.6	7	N. America
Q. Gambelii		6.9	9	N. America
Q. macrocarpa	12 ± 1	6.9	6	N. America
Q. bicolor	12	7.4	3	N. America
Q. montana	12	7.3	3	N. America
Q. Sargentii ×		7.1	7	
Q. prinoides		6.9	3	N. America
Q. Muhlenbergii	12	6.8	7	N. America
Q. aliena		7.0	4	Asia
Q. glandulifera		7.1	9	Asia
Q. mongolica	12 ± 1			Asia
Q. dentata		11.2	80	Asia
Q. dentata		8.7	8	Asia

Q. ludoviciana = Q. phellos × rubra.
Q. Leana = Q. imbricaria × velutina.
Q. exacta = Q. imbricaria × palustris.
Q. Bebbiana = Q. alba × macrocarpa.
Q. Sargentii = Q. montana × robur.

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NOTULAE SYSTEMATICAE AD FLORAM SINENSEM, II[1]

H. H. HU

Acer Chingii, sp. nov.

Arbor ad 11 m. alta, trunco 60 cm. diam. ,coma ampla patente, cortice calcareo-albido, ramulis glabris. Folia 5-loba, circa 10 cm. diam., basi profunde angusteque cordata, lobis acuminatis integris vel apicem versus sparse adpresseque serratis, lobo medio anguste oblongo marginibus fere parallelis ad 5.5 cm. longo et 2 cm. lato, lobis lateralibus ad 4.5 cm. longis, basalibus ovatis 1–1.2 cm. longis, saepe deorsum curvatis lateribus inferioribus fere contiguis, utrinque reticulata, supra laete viridia et glabra, subtus nervis primariis basin versus satis dense villosis exceptis glabra; petioli ad 3 cm. longi, pubescentes. Corymbi fructiferi circa 5 cm. diam., ut videtur breviter paniculati et multiflori, sed in specimine viso fructus immaturos 4 vel 5 gerentes; flores ignoti; samara alis angulo recto divergentibus nuculo leviter compresso 4 mm. longo incluso ad 18 mm. longis et 7 mm. latis rubro-purpureis extus rectis intus leviter falcatis basin versus angustatis.

Tree to 11 m. high, trunk 60 cm. in diam., with large spreading crown, bark chalky white, branchlets glabrous. Leaves 5-lobed, deeply cordate at base, 10 cm. in diameter, lobes acuminate, entire or sparsely and appressedly serrate toward the apex, midlobe to 5.5 cm. long, 2 cm. broad, lateral lobes to 4.5 cm. long, basal lobes often bending abruptly downward, approximately 10–12 mm. long, reticulate, light green and glabrous above, glabrous except densely pubescent along the midribs beneath; petiole to 3 cm. long, pubescent; corymbs about 5 cm. in diameter, apparently many-flowered, in the specimen at hand with 4 or 5 fruits; flowers unknown; samara with wings spreading at right angle, 1.8 mm. long including the nutlet, wings reddish-purple, straight at back, slightly falcate on the inner side, narrowed at base, to 14 mm. long, 7 mm. broad; nutlet slightly compressed, smooth, 4 mm. long.

KWANGSI: Bin Long, Miu Shan, north of Luchen Hsien, on border of Kweichow, alt. 1220 m., common in woods, *R. C. Ching*, Kwangsi Expedition, Academia Sinica, no. 5980 (type), June 14, 1928.

A species of the section Platanoidea, distinct from other Asiatic species chiefly in the deeply cordate base of the leaf and approximate basal lobes.

Schima bambusifolia, sp. nov.

Arbor ad 15 m. alta, trunco 30 cm. diam.; ramuli glabri. Folia coriacea, elliptica vel elliptico-lanceolata, 5.5–9 cm. longa et 2–2.5 cm. lata, acuta vel longe acuminata, basi cuneata vel fere rotundata, integra vel obscure crispata ad marginem, supra levia, glabra, lucida et intense viridia, subtus glabra et obscure coeruleo-viridia; petioli crassi, 13 mm. longi, glabri. Fructus racemosi, globosi, 1 cm. diam., brunnescentes, albido-punctati; pedicellis crassiusculi, 12 mm. longi; semina reniformia, 5 mm. longa et 4 mm. lata, uno latere leviter conçava, anguste alata.

[1] Continued from p. 48.

Tree to 15 m. high, trunk 30 cm. in diam.; branchlets glabrous. Leaves coriaceous, elliptic to elliptic-lanceolate, acute to long acuminate at apex, cuneate to subrounded at base, entire to obscurely crisped along the margins, smooth, glabrous and dark shining green above, glabrous and dull bluish-green beneath, 5.5–9 cm. long, 2–2.5 cm. broad; petiole thick, 13 mm. long, glabrous. Fruits racemose, globose, 1 cm. in diam., brownish, punctate with whitish dots; pedicels thickish, 12 mm. long; seeds reniform, slightly concave on one side, narowly winged, 5 mm. long, 4 mm. broad.

A species differing from all others in much smaller entire leaves, smaller fruits and seeds.

KWANGSI: Shih wan dar Shan, south of Nanning, alt. 1300 m., common in woods, *R. C. Ching*, no 8020, Oct. 19, 1928 (type), no. 8523, Oct. 27, 1928.

Vatica cordata, sp. nov.

Planta lignosa scandens (fide coll.), ad 4 m. alta; ramuli glabri longitudinaliter striati, lenticellis sparsis elevatis breviter ovalibus instructi, ut inflorescentia luteo-griseo-pubescentes. Folia subcoriacea, oblongo-ovata, 12–14 cm. longa et 7–9.5 cm. lata, basi cordata et 5-nervia, supra glabra et pallide viridia, subtus pallidiora et dense pilis flavo-fuscis sericeo-strigosis; petioli 5–6 cm. longi, glabrescentes. Inflorescentia axillaris, racemosa, folia excedens; alabastra conica, obtusa, 4.5 cm. longa, puberula; bracteolae ovato-lanceolatae, acutae, 1.5 mm. longae; calycis lobi deltoidei, acuti, 1 mm. longi. Fructus calyx tubo brevi sparse puberulo; calycis lobi longiores 2, lineari-oblongi, 7.5 cm. longi et circa 1–2 cm. lati, obtusi vel subacuti, basin versus leviter sensim angustati, minute pilosuli, nervis 3 conspicuis et 2 lateralibus levioribus dimidios lobos tantum percurrentibus; lobi breviores 3, oblongi, 1.5 cm. longi et 4 mm. lati, acuminati et apicum versus dentibus 1 vel 2 instructi; fructus obovoidei, apice rostrati, circa 1.8 cm. longi et 6 mm. diametientes.

Woody climber (fide collector) to 4 m. high, branchlets glabrous, longitudinally striated, with scattered elevated short oval lenticels, branchlets and inflorescence yellowish-gray pubescent, leaves subcoriaceous, oblong-ovate, cordate and 5-veined at base, glabrous and light green above, paler and densely yellowish-brown sericeous-strigose beneath, 12–14 cm. long, 7–9.5 cm. broad, petiole glabrescent, 5–6 cm. long; inflorescence axillary, racemose, longer than leaves; flower buds conical, obtuse, 4.5 mm. long, puberulous; bracteoles ovate-lanceolate, acute, 1.5 mm. long; calyx-teeth deltoid, acute, 1 mm. long; pedicels to 12 mm. long, puberulous; fruiting calyx with short tube sparingly puberulous, large calyx-lobes 2, linear-oblong, obtusish or subacute at apex, slightly narrowed gradually downward, minutely pilosulous, with three strong veins in the middle portion and 2 fainter lateral veins reaching about half of the length of the wings, 7.5 cm. long, about 12 mm. broad, smaller lobes 3, oblong, acuminate and 1- or 2-auricled near the apex, 1.5 cm. long,

4 mm. broad; fruit obovoid, beaked at apex, about 1.8 cm. long, 6 mm. in diameter.

KWANGSI: Bako Shan, west of Poseh Hsien, alt. 900 m. in thicket on cliff, *R. C. Ching*, Kwangsi Expedition, Academia Sinica, no. 7426 (type), Sept. 14, 1928.

A species of the section Synaptea distinct from other species chiefly in the ovate-oblong leaves cordate at base and densely yellowish green sericeous-strigose beneath. That this species is recorded by the collector as a woody climber is exceedingly interesting. If correct, then it may prove to be the first known species of this family to be climbing, and the slightly bending branches certainly look like those of climbers.

This is the second species of the genus *Vatica* discovered in China. The other species, *V. astrotricha* Hance, endemic in Cochin-China but lately discovered in Hainan, also belongs to this section. With the discovery of this species, there are now discovered in China three species of the family Dipterocarpaceae. The third species of this family is *Shorea chinensis* which Merrill discovered in Kwangtung.

Gilibertia angustiloba, sp. nov.

Frutex ad 1.5 m. altus (fide coll.), ramulis glabris. Folia omnia (?) profunde trilobata, ad 16 cm. longa, basi cuneata vel sub-rotundata, glabra, supra laete viridia, subtus pallidiora, lobis lanceolatis, medio ad 15 cm. longo, lateralibus ad 12 longis, omnibus circa 18 mm. latis et apicem versus angustatis acutis, leviter et sparsissime denticulatis denticulis mucronulatis vel integris, nervo medio supra elevato et angusto, subtus minus elevato sed latiore, venulis exilibus, non reticulatis; petioli ad 6.5 cm. longi. Fructus (immaturi) globosi, 4 mm. diam., glabri, calyce obsolete denticulato, disco conspicuo, stylis in columnam 1 cm. longam connatis; pedicelli circa 1 cm. longi.

Shrub to 1.5 m. high (fide collector), branchlets glabrous; leaves all (?) deeply 3-lobed, cuneate to rounded-cuneate at base, to 16 cm. long, glabrous, bright green above, paler beneath, lobes lanceolate, mid-lobe slightly longer than the lateral lobes, all tapering toward the apex, acute, obscurely and very remotely denticulate or entire, teeth mucronate, midrib elevated and narrow above, less elevated but broader beneath, veinlets faint, not reticulate, mid-lobe to 15 cm. long, lateral ones to 12 cm. long, about 18 mm. broad; petiole to 6.5 cm. long; fruit (immature) globose, glabrous, 4 mm. in diameter, crowned with a prominent disk, calyx-teeth obsolete, style connate, 1 mm. long; pedicels about 1 cm. long.

KWANGSI: Shih Wan Dar Shan, south of Nanning, alt. 900 m., under growth in forest, *R. C. Ching*, Kwangsi Expedition, Academia Sinica, no. 8019 (type), Oct. 19, 1928.

A species distinct in its leaves being all (?) deeply 3-lobed with long narrow remotely denticulate lobes which have a prominent midrib and faint veinlets.

Sinojackia Rehderiana, sp. nov.

Frutex ad 5 m. altus; ramuli juveniles stellato-pubescentes. Folia membranacea, subsessilia vel breviter petiolata, obovato-elliptica ad elliptico-oblanceolata vel oblonga ad ovata, ad 9 cm. longa et 4 cm. lata, sed plerumque multo minora (2–3 cm. longa et 1.2–1.5 in ramis florentibus), acuta vel obtusiuscula, basi cuneata vel rotundata vel subcordata, laete viridia, utrinque ad venas et laminae basin versus stellato-pubescentia, ceterum glabra, reticulata; petioli breves, 1–4 mm. longi, stellato-pubescentes. Flores albi, penduli, laxe cymoso-paniculati, pedicellis ad 2 cm. longis et pedunculis gracillimis dense stellato-pilosis, calyx cinereo-stellato-pubescens; 5–6-dentatus dentibus triangularibus acutis 1 mm. longis; corolla profunde 5–6-partita segmentis oblongo-ellipticis, 12 mm. longis et 4 mm. latis, acutiusculis, extus stellato-puberulis; stamina 8 mm. longa, filamentis basi in tubum brevem connatis stellato-puberulis; ovarium 3-loculare, stellato-puberulum, sensim in stylum 6 mm. longum, glabrum, attenuatum, stigmate obsolete 3-lobulato; ovula 8 in quoque loculo, biseriata. Fructus ligneus, indehiscens, apice conico longe rostrato ad 1 cm. longo; pars inferior obovoidens, leviter compressus, in stipitem attenuatus et cum stipite 1.5 cm. longum et 5.5 mm. diam., exocarpio suberosa non fisso, endocarpio ligneo, semen solitarium.

Shrub to 5 m. high; young branchlets stellate-pubescent. Leaves membranaceous, subsessile to short-petioled, obovate-elliptic, elliptic-oblanceolate, oblong to ovate, acuminate, acute or obtusish at apex, cuneate, rounded or slightly cordate at base, serrulate, green and glabrous except sparsely stellate-pubescent along the main veins or at the base of leaves on both surfaces, veins reticulate, to 9 cm. long, 4 cm. broad, usually much smaller (2–3 cm. long, 1.2–1.5 cm. broad at flowering time); petiole short, 1–4 mm. long, stellate-pubescent. Flowers white, pendulous, loosely cymose-paniculate, peduncles and pedicels very slender, densely stellate-pilose, pedicels to 2 cm. long; calyx grayish stellate-pubescent, 5–6-dentate, teeth triangular, acute, 1 mm. long; corolla deeply 5–6-cleft, segments oblong-elliptic, acutish at apex, stellate-puberulous outside, 12 mm. long, 4 mm. broad; stamens 8 mm. long, filaments connate at base into a short tube, stellate-puberulous; ovary lanceolate, stellate-puberulous, 3-celled, style subulate, 6 mm. long, stigma obscurely 3-lobed; ovules 2-seriate in each cell, 4 in each series. Fruit woody, indehiscent, apex conical, long-beaked, to 1 cm. long, lower half of the fruit obovoid, slightly compressed, tapering into a stalk at base, grayish brown, punctate with whitish dots, 15 mm. long with the stalk, 5.5 mm. broad; exocarp corky, not fissured; endocarp woody; seed solitary.

Allied to *S. xylocarpa* Hu, differing in shrubby habit, in thinner leaves, in looser flowers and much more slender and elongated fruits.

KIANGSI: Nanchang, common on low hills, *H. H. Hsiung*, no. 578, in 1929 (fruiting specimen); no. 578b, April 20, 1930 (flowering specimen; type).